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UNITED STATES DEPARTMENT OF AGRICULTURE

DEPARTMENT BULLETIN No. 1286

Washington, D. C. ▼ December 10, 1924

SOUTH AMERICAN LEAF DISEASE OF PARA RUBBER

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INTRODUCTION

The revival of interest in rubber cultivation in the American Tropics following a long period of indifference has stimulated a review of past attempts and a study of the factors which may determine the success or failure of new enterprises. Unfortunately, the earlier efforts in tropical America were largely expended before the rubber-planting industry was established upon a scientific and practical basis. Thus many ill-advised, quickly organized, and inflated enterprises sank millions of dollars in plantings of Castilla and other less suitable rubber trees, which could not compete with the rapidly expanding Hevea rubber culture of the Far East. The subsequent drop in rubber prices, the loss of confidence on the part of shareholders, and the relatively favorable returns from such crops as coffee, coconuts, and cacao led to a general abandonment of the rubber plantations. The industry gradually declined, so

[1] The writer wishes to express his thanks to Director W. G. Freeman, W. Nowell, F. W. Urich, and others, of the Trinidad Department of Agriculture; to Sir J. B. Harrison, R. Ward, A. Abraham, and others, of the British Guiana Department of Science and Agriculture; to Dr. Gerold Stahel and A. Reyne, of the Departement van Landbouw, Suriname; and to E. A. Robinson, owner of the Non-Pariel rubber plantation, Trinidad, for their most generous help and information and for plant-propagating material brought to the Panama Canal Zone.

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that to-day in many districts there are left only occasional deserted plantings.

Although the superior Para rubber (*Hevea brasiliensis* (Mull.) Arg.) was tried in a few plantings which survive even now in Mexico, Nicaragua, Panama, Colombia, Venezuela, and the West Indies, it was mainly in the Guianas and Brazil that this species was utilized almost exclusively from the beginning. Here, unfortunately, in the general region which includes the native habitat of the tree the formerly very promising industry of the Guianas has been nearly ruined by the ravages of a destructive endemic leaf disease which spread from the scattered wild trees of the jungle to the thickly planted plantations. Although this disease, known generally as the South American leaf disease (*Dothidella ulei* P. Henn.), has received considerable attention from local botanists, it seemed desirable, in view of the increasing interest in rubber planting in Central America and South America, to determine its present status, possibilities of control, and to what extent it may become a menace to renewed planting enterprises. For this purpose the writer was sent to Trinidad and the Guianas during the summer of 1923 to make a survey of the disease situation. The results, together with a general review of previous investigations, are incorporated in this bulletin.

HISTORY AND GEOGRAPHIC DISTRIBUTION OF THE DISEASE

The South American leaf disease was first reported in 1904 by P. Hennings (*11*),[2] who published a short description of the causal fungus from diseased leaves collected from wild trees of *Hevea brasiliensis* in 1901 and 1902 by E. Ule in the upper region of the Amazon, near Jurua (Acre Territory), on the banks of the Rio Jurua Mirum (Acre Territory), and along the Amazon proper near Iquitos, Peru (fig. 1). Hennings named the perithecial form *Dothidella ulei* and a pycnidial fungus, which appeared to be merely another stage on the same leaves, *Aposphaeria ulei*. The disease caused defoliation of the attacked leaves and was considered very injurious. Attention was called to the danger of its possible appearance in Hevea cultivations.

The literature contains no further reference to this disease until 1910, when A. W. Drost (*6*) briefly described a leaf trouble on nursery plants at Paramaribo, Dutch Guiana. Drost observed, in addition to pycnidia, a "Ramularia-like" conidial stage, but made no further effort toward its identification. His description of the symptoms, however, leaves little doubt that he was dealing with the disease in question. It was considered indigenous, having been found on the related *Hevea guyanensis* in its native habitat in the forests. In addition to the leaves, it was observed to attack young stems and twigs, causing warty swellings. The trouble was not considered serious.

In 1911 Kuyper (*13*) published a more detailed description of the trouble in Dutch Guiana and mentioned its occurrence throughout the country both on plantations of *Hevea brasiliensis* and on

[2] Serial numbers (*italic*) in parentheses refer to "Literature cited," at the end of this bulletin.

the wild *Hevea guyanensis* in the jungles. He found the conidial stage to be a Fusicladium, which he figured and named *F. macrosporum*. He also figured and described the associated pycnidial fructification, but was unable to find perithecia. Various attempts

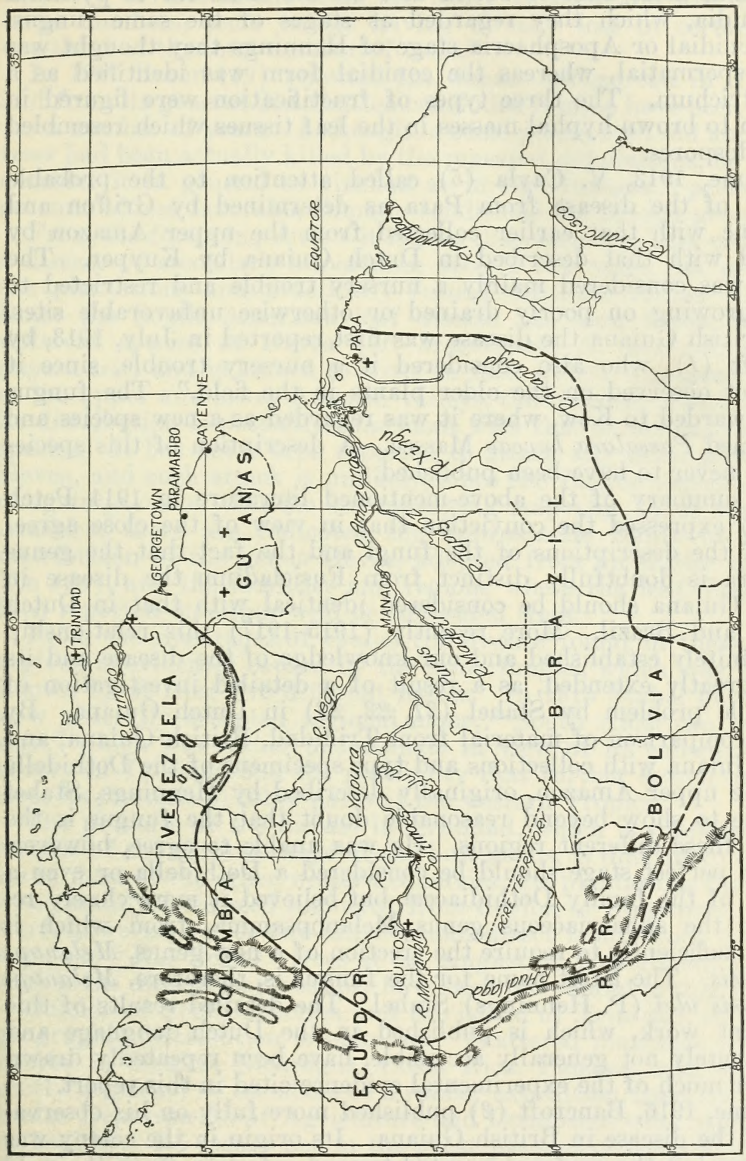


FIG. 1.—Map of the Amazon region, showing the distribution of native Hevea trees. The heavy broken line follows approximately the known limits of distribution of the genus Hevea, which is largely confined to the lower altitudinal jungles of the Amazon and its tributaries, as adapted from Ule. The crosses indicate the regions where the South American leaf disease has been reported, viz, Brazil, Peru, the Guianas, and Trinidad. In the island of Trinidad the disease has apparently been introduced along with planting material

to grow the fungus in artificial culture failed. The disease appeared very irregularly, and although it was rather severe on the weaker individuals he considered the damage slight. Nevertheless, in one case trees 6 years old were found to have succumbed from the frequent defoliation.

Specimens of a leaf disease collected in 1912 by V. Cayla on cultivated Hevea at Para, Brazil, and sent to Griffon and Maublanc (*8*) were found to be attacked by the same fungus described earlier from Brazil by Hennings, *Dothidella ulei*. In addition to the Dothidella, these authors found also on the same leaves pycnidia and conidia, which they regarded as stages of the same fungus. The pycnidial or Aposphaeria stage of Hennings they thought was merely spermatial, whereas the conidial form was identified as a Scolecotrichum. The three types of fructification were figured in addition to brown hyphal masses in the leaf tissues which resembled chlamydospores.

In June, 1913, V. Cayla (*5*) called attention to the probable identity of the disease from Para as determined by Griffon and Maublanc with that earlier collected from the upper Amazon by Ule and with that described in Dutch Guiana by Kuyper. The disease was considered mainly a nursery trouble and restricted to plants growing on poorly drained or otherwise unfavorable sites.

In British Guiana the disease was first reported in July, 1913, by Bancroft (*1*), who also considered it a nursery trouble, since it "was not observed on the older plants in the field." The fungus was forwarded to Kew, where it was regarded as a new species and was named *Passalora heveae* Massee. A description of this species appears never to have been published.

In a summary of the above-mentioned literature in 1914 Petch (*15*, *16*) expressed the conviction that in view of the close agreement of the descriptions of the fungi and the fact that the genus Passalora is doubtfully distinct from Fusicladium the disease in British Guiana should be considered identical with that in Dutch Guiana and Brazil. More recently (1915–1917) this relationship was definitely established and our knowledge of the disease and its effects greatly extended, as a result of a detailed investigation of the whole problem by Stahel (*21*, *22*, *23*) in Dutch Guiana. By careful comparison of material from Trinidad, British Guiana, and Dutch Guiana with collections and type specimens of the Dothidella from the upper Amazon, originally described by Hennings, Stahel was able to show beyond reasonable doubt that the fungus is the same in these different regions. He was unable to agree, however, that the perfect stage should be considered a Dothidella or even a member of the family Dothidiaceæ, but believed it more closely related to the sphaeriaceous genus Melanopsamma, from which it differed sufficiently to require the erection of a new genus, *Melanopsammopsis*. The latest name for the fungus is, therefore, *Melanopsammopsis ulei* (P. Hennings) Stahel. The detailed results of this important work, which is published in the Dutch language and unfortunately not generally accessible, have been repeatedly drawn upon for much of the experimental evidence cited in this report.

In June, 1916, Bancroft (*2*) published more fully on his observations of the disease in British Guiana. Its origin in the colony was unknown; but the evidence pointed toward infection from the wild Heveas, of which at least two species had been observed to suffer from the trouble in the forest, *Hevea confusa* and an undetermined species. The disease occurred in all parts of the country but was less common on or near the coast lands. It was also most prevalent where large areas of pure Hevea were being grown.

Reporting the following year (*3*) upon a visit to rubber plantations in Dutch Guiana, Bancroft viewed the situation as a whole still more seriously and predicted the eventual abandonment of rubber culture in these countries. In Dutch Guiana, he stated, "on the majority of estates the trees are badly affected and are dying in large numbers, some estates having already lost in certain areas one-third of the total number of trees."

In 1917 Rorer (*19*) reported the disease widespread in Trinidad and from its general distribution concluded it must have been present for a number of years. Although in some places both old and young trees had been actually killed by the repeated defoliations, he did not consider it in general so virulent as in the Guianas, "probably on account of less favorable climatic conditions for fungus growth."

From the foregoing review it is seen that what was first considered a disease of secondary importance after a few years has spread in the plantations and practically ruined the local rubber industry. Since the South American leaf disease has been found on three different species of Hevea (*H. brasiliensis*, *H. confusa*, and *H. guyanensis*) and is known to occur in such widely separated regions as the upper and lower Amazon valleys, the Guianas, and Trinidad, its distribution is probably coincident with that of the native Hevea species. It has never been reported to attack any other plant than Hevea, and such attack is unlikely, since the fungus seems to be an obligate parasite. On the accompanying map (fig. 1) of equatorial America, there are indicated the approximate limits of natural distribution of the genus Hevea, adapted from an earlier chart by Ule (*26*), and the localities and regions where the leaf disease has been reported on either wild or cultivated trees.

From the researches of Stahel the disease found in these remote regions is evidently caused by the same fungus, which was hitherto known by at least five different names. In 1915 Stahel gave it the now generally accepted regional name, "South American leaf disease," which was rather unfortunate in view of its subsequent discovery in Trinidad and the possibility that further search may disclose its presence in other parts of the western Tropics.

The presence of the disease in Trinidad, which is supposed to lie outside of the natural range of the host genus, is difficult to explain. As in most of the other western countries, the plantations there have come mainly from seed imported from Ceylon or Singapore. There were, however, one or two importations direct from South America, e. g., the "Rio Negro" trees at St. Augustine Experiment Station; so that the disease may possibly have been introduced in this way.

Outside of South America and the island of Trinidad, its further geographic distribution is unknown. Scattered plantings of Hevea rubber in Mexico, Nicaragua, Costa Rica, Panama, and Haiti recently inspected by members of a rubber expedition from the United States Departments of Agriculture and Commerce were reported to be healthy. Its occurrence in the great plantation areas of the Far East is unlikely, since the fungus is apparently not very well adapted to withstand prolonged inactivity. Nothing even remotely suggesting the characteristic symptoms of this disease was observed by the writer while inspecting a large number of rubber estates on the islands of Java and Sumatra during the years 1919 to 1921. This is

corroborated with respect to the Federated Malay States by Belgrave (*4*), who published a report on the leaf disease following a short visit to Trinidad and British Guiana in 1921. In his recent treatise on the diseases of rubber Petch (*17*, p. 78–81) likewise affirms that this leaf disease is confined to the American Tropics.

PRESENT STATUS OF THE DISEASE

TRINIDAD

Although Rorer (*19*) found the South American leaf disease widespread throughout the island of Trinidad in 1916, it has not been solely responsible for the lack of expansion of the rubber plantation industry there. A brief survey of agricultural development of the island during the last two decades shows that interest in rubber probably began to wane not only before the leaf disease was known but even before much Hevea was planted. In a comprehensive report on rubber cultivation in Trinidad and Tobago by a special committee of the local Board of Agriculture in 1917 (*14*), it was shown that some rubber had been planted on at least 155 estates, of which most had unfortunately used Castilla, Hevea having been planted "except in a very few instances, only upon an experimental scale, or among cacao or along the edges of cacao fields." This mistake in the use of the wrong species of rubber plant seems not to have been fully realized until the period of high prices had practically passed; but, combined with the inducements offered in cacao, sugar cane, and coconuts, it gave rubber planting a setback from which it has apparently never recovered.

When the writer visited the island of Trinidad he found that most of the Castilla and Funtumia (also considered undesirable) had been cut out and that many of the scattered Hevea plantings were in a derelict condition. In some of these, especially in the southern districts, leaf disease was rampant at the time, as shown by the slow growth, die-back, and ragged, shot-hole appearance of leaves. (Pl. II, fig. 1.) Even here, scattered trees along the roadside in more exposed sites showed nearly normal development. In the northern district the small government gardens on River Estate and at the St. Clair and St. Augustine experiment stations near Port of Spain seemed to have suffered but little, although young seedlings springing up beneath the same trees and in near-by nursery beds were often badly infected. Likewise, on the eastern coast, where the only plantings of considerable extent occur and are now being tapped, the disease has been of small consequence. The Non-Pariel and Rydal Hall estates, on which nearly 50,000 trees, mostly in pure stands, occur, give one much the same impression as any well-kept Far Eastern plantation. (Pl. I.) Although rather closely spaced, the trees as a rule are well developed, and the yields of first-quality smoked sheet are said not to be under those of similar estates in the Orient. Even here numerous young seedlings in the drainage ditches and along the edges of the fields were generally infected with the leaf disease. On the 10 to 16 year old mother trees, however, no evidence of repeated earlier defoliations and the consequent die-back or of leaf attack at the time was observed. The probable reason for this fortunate state of affairs is found in a climatic difference discussed fully under a later heading.

Viewing the situation in Trinidad as a whole, although the leaf disease has doubtless been a discouraging factor in contemplated extension of rubber culture in certain parts of the island, in the eastern territory it has been of little consequence.

BRITISH GUIANA

In British Guiana most of the rubber has been planted on river lands at 100 to 200 feet elevation, and rarely does any occur more than 60 miles inland from the coast. Figures published annually in the Reports of the Department of Science and Agriculture show a steady decrease of acreage in production since 1917, when the South American leaf disease became generally prevalent. Owing to the ravages from this disease and the consequent abandonment of extensive areas, the export of rubber decreased from 20,384 pounds in 1920 to 1,568 pounds in 1921 (*7*, p. 11). The department's station at Christianburg had to be abandoned, as 95 per cent of the trees was seriously affected by the disease, which later became prevalent at Issorora, the yield of dry rubber from tapped trees having fallen from 4.97 pounds in 1919 to 2.4 pounds in 1920. Trees which have been at all seriously affected by the disease never recover their original vigor. Although seriously injuring the foliage of the wild rubber trees (*Hevea confusa*), the disease did not appear to exert on them the intensely destructive action it did on *Hevea brasiliensis* (*9*, p. 16).

Rubber in British Guiana was planted largely in pure stands, which in many cases were surrounded by belts of jungle left to protect the trees from storms and winds. Such a situation furnished ideal conditions for the spread of the leaf disease to the plantings from its native habitat on the scattered wild rubber trees of the adjacent jungles. According to the present director of agriculture, Sir J. B. Harrison, the leaf disease has always been more severe in such protected plantings, whereas trees on exposed hills or higher land were generally less affected. Likewise, the rubber trees on low-lying coast areas exposed to sea breezes, where also owing to poor soil growth was slower, were noticeably less affected than the up-river estates.

Some deserted plantings inspected by the writer on the lower Essequibo River showed strikingly the effects of the disease. One very dense planting about 12 years of age seemed to have suffered little until the last year or two, since the trunks were of normal size. At the time of examination, however, some of the trees showed numerous dead branches, and scarcely a half-grown leaf could be found which was not distorted or badly spotted, indicating a belated infection. Other trees with mostly mature leaves would have been considered as yet unattacked had there not been occasional dead branch tips indicating repeated defoliations last year.

In a younger planting, 4 to 6 years of age, less than a quarter of a mile distant from the above, the disease was seen in its most active stage during an epidemic which had apparently been in progress for two weeks. Fully half the trees had just passed the "wintering" period and were developing new leaves, which averaged from a few days to a week or more in age. As pointed out by earlier writers, this period is less defined in the South American

countries than in the Far East. In the Guianas it is said to require three to four months' time before all the trees in a planting have lost their old leaves and grown new ones. Large variations also occur between different branches on the same tree in the time of dropping their old leaves.

As noted on July 24, the foliage of this younger planting was everywhere discolored, twisted, or crumpled, and falling off. (Pl. III, fig. 1.) In most cases the leaflets had dropped in advance of the long, slender petioles, giving the ends of the branches a peculiar bristly appearance. (Pl. III, fig. 2.) On other trees the naked succulent branch tips themselves were discolored, and stem swellings farther back indicated still earlier infections. A number of trees had died the year before and the amount of die-back, although less evident on account of the defoliated condition of the trees, was nevertheless outstanding enough to show that the planting had suffered seriously in the past. A more ruinous condition could scarcely be imagined. The disastrous effect on the flow of latex from the repeated defoliations in combination with relatively high labor prices has naturally made further tapping unprofitable, a situation which is said to exist practically throughout the colony.

DUTCH GUIANA

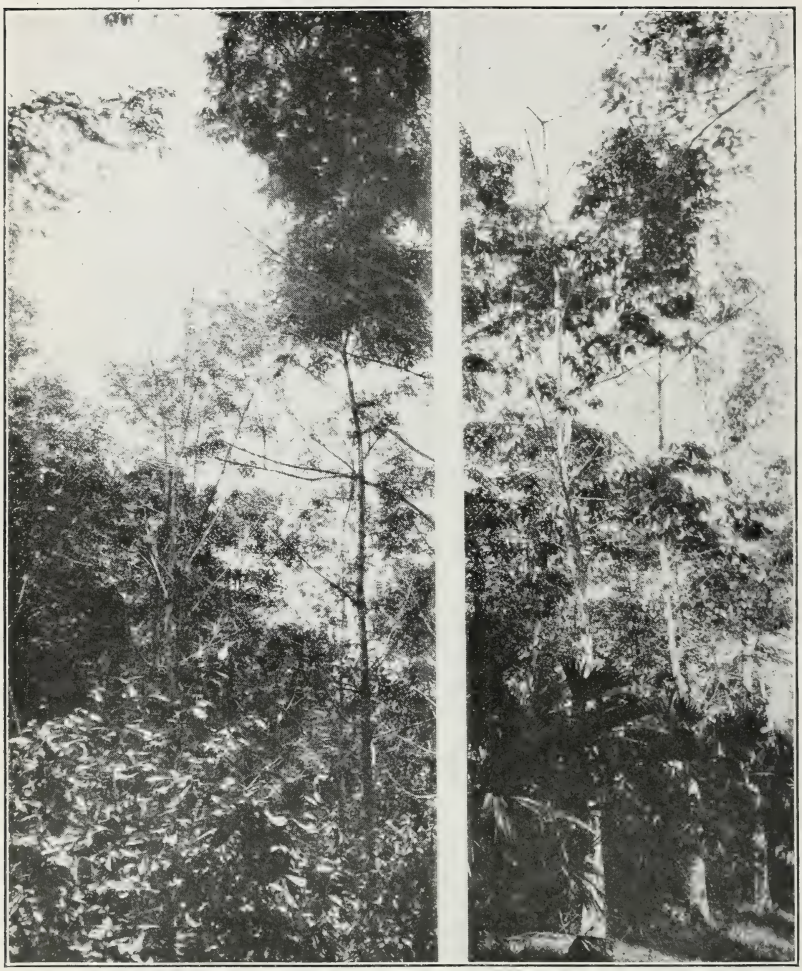
The condition of rubber cultivation in Dutch Guiana appears to be even more serious than in British Guiana. Bancroft (*3*) called attention to this in 1917. A probable explanation is found in the relative positions of the plantings in the two countries with reference to the seacoast, those in Dutch Guiana having generally been farther inland, away from the protective effect of the coastal winds, than those in British Guiana. Also the plantings in Dutch Guiana were in closer proximity to the indigenous *Hevea guyanensis*, which everywhere in the jungle was naturally infected with leaf disease.

As in British Guiana, the industry here has been practically abandoned. Two reasons for this are commonly given, the great reduction in yield on account of the leaf disease and high labor prices. The net result is a production cost which makes competition with other countries nearly impossible. About 3,000 acres were originally planted with Hevea; but, in contrast with the industry in British Guiana, this was mostly in mixed culture interplanted with coffee. In recent years most of the trees not killed by the leaf disease on several estates have been cut out to improve the condition of the coffee or other intercrop.

In a small planting on the experiment station farm at Paramaribo the disease was observed in its typical form, though it was not at the time in a very active stage. The amount of die-back caused by earlier defoliations is indicated in Plate II, Figure 2. Here the writer conferred with Dr. Gerold Stahel, director of the experiment station, whose valuable researches on the leaf disease have already been mentioned. Although, for lack of time, very little rubber was personally inspected, the impression gained from conferences with various officials and business men indicated little hope for the future of rubber cultivation in the colony.

A HEALTHY PRODUCING RUBBER ESTATE 12 TO 14 YEARS OLD ON THE EASTERN COAST OF TRINIDAD

Although the South American leaf disease was found affecting volunteer seedlings growing beneath the trees in this and adjacent plantings, the larger trees have not suffered and have been regularly tapped for a number of years



HEVEA RUBBER PLANTINGS RUINED BY THE LEAF DISEASE

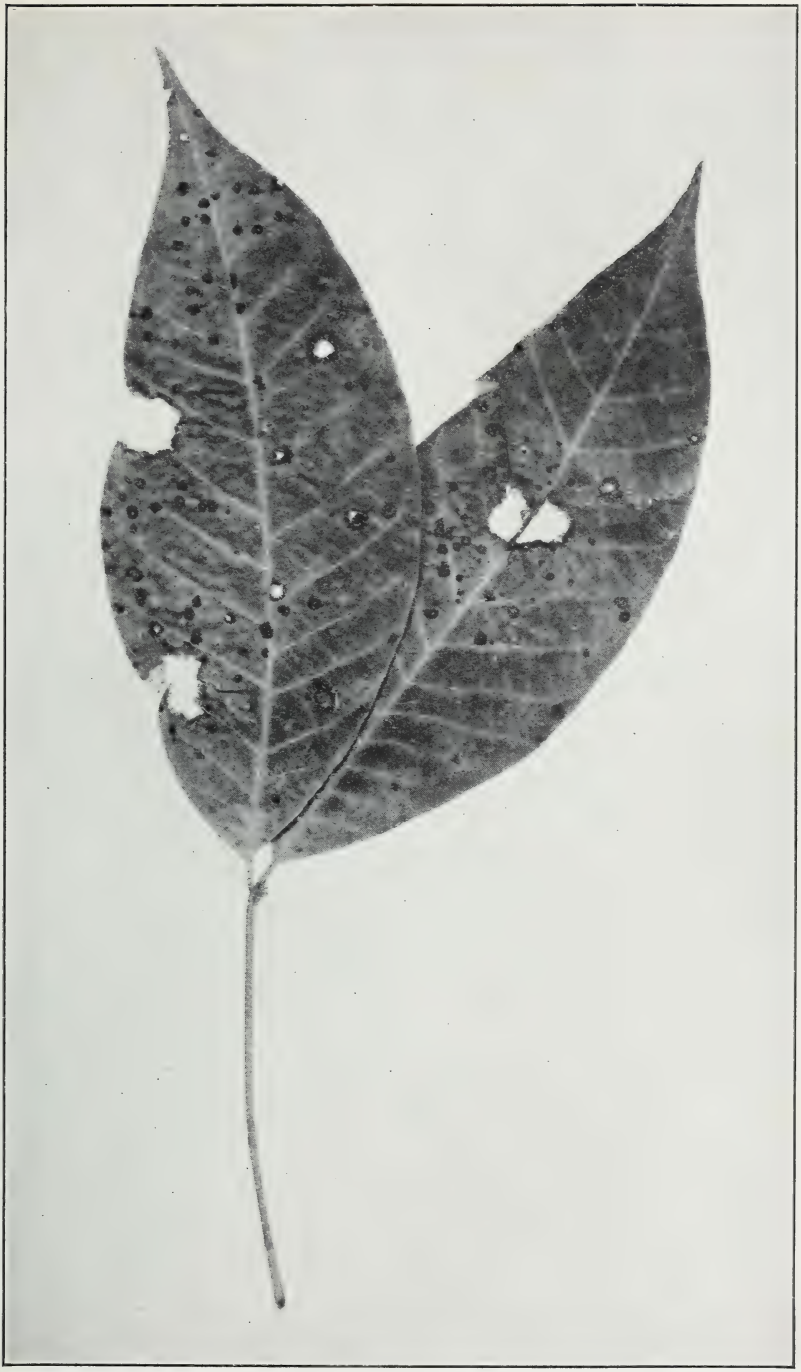
FIG. 1.—This view (at left), from the southern portion of the island of Trinidad, shows rubber trees, interplanted with cacao, which have been repeatedly defoliated by the leaf disease. Many of the branches have recently died back, while on other trees, as in the upper left-hand corner of the illustration, the foliage has the characteristic thin appearance because of stunting, distortion, and loss of occasional leaflets. FIG. 2.—A rubber planting in Dutch Guiana (at right), which illustrates the typical result of prolonged attack from the leaf disease. All but a few of the branches of these trees, 10 to 12 years old, have died back, and the trunks scarcely approximate in size a normally developed 5-year-old tree

YOUNG SHOOTS OF HEVEA SEVERELY ATTACKED BY THE LEAF DISEASE

FIG. 1.—(At left.) The tender, very young unfolding leaves have been blackened and killed, although an earlier spray of leaves which apparently passed the susceptible stage during a period unfavorable for infection is healthy and vigorous. FIG. 2.—(At right.) The dead leaflets have dropped off, leaving the slender naked petioles, which usually persist a few days longer

TYPICAL SYMPTOMS OF THE DISEASE ON THE MATURE LEAF

Although infection doubtless took place when the leaf was very young, growth in this case continued, resulting in a stunted, shot-hole appearance. The affected portions have died, and around the margins of the holes and spots black fruiting bodies of the fungus have developed. (Natural size)



CHARACTERISTIC "PEPPERING" OF LEAF INFECTED AT A LATER STAGE

Most of the spots here have failed to enlarge on account of practical immunity of the tissues after the leaf is a week or more old. The minute black stromatic rings are characteristic of the disease

MAGNIFIED PORTION OF A LEAF, SHOWING DETAILS OF THE STROMATIC RINGS

The black masses and circles consist of large numbers of minute spherical fruiting bodies of the fungus, the pycnidia and perithecia. They break through the upper surface of the leaf and may occur singly or fused laterally in groups, arranged around the border of the spot. (Magnification × 7)

DESCRIPTION OF THE DISEASE

The leaf disease appears first on the tender, pendent, very young (3 to 5 days old) leaves as opaque olive-green spots, 1 to 5 centimeters in diameter, on the naturally translucent reddish brown surfaces of the leaflets. When many spots develop the leaflets soon blacken, shrivel up, and fall off, followed in a few days by the long naked petioles. (Pl. III.) A severe general attack at this stage gives much the same impression as a case of Phytophthora leaf fall, except, of course, that it is confined to the very young leaves. Since, following the annual "wintering" period, the trees put out new leaves over the entire crown or at least over entire branches at approximately the same time, it is clear how a severe attack of the disease at this crucial stage can cause complete defoliation. In the course of four to five weeks after the first defoliation the trees have again put out a new crop of leaves, which in turn may be killed and drop off. Thus, the planting appears to be continuously going through the wintering process. Stahel (*23*) found that three successive defoliations, occurring over a period of about six months, were sufficient to cause a general dying back of the entire crowns of 5 to 6 year old trees. This die-back, which is generally an indication of the presence of the leaf disease in a planting, was shown to be due to local starvation resulting from depletion of the starch reserves, first in the smaller branches and finally, with repeated defoliation, in the larger limbs and even in the trunk itself. Reduction in the yield of rubber follows closely the exhaustion of reserve food materials, so that after a few defoliations tapping becomes unprofitable.

Less severe attacks of the disease usually cause only the shedding of occasional leaflets, which, combined with more or less stunting of the remainder, gives the foliage a peculiar thin appearance. When only a few spots develop on a very young leaf the unaffected portions continue to grow and cause a characteristic crumpled appearance. (Pl. III, fig. 1.) The subsequent falling out of the diseased portions, especially of the marginal ones, on such leaves gives them a ragged shot-hole aspect, which persists until the following wintering period. (Pls. IV and V.) This frayed-out condition is typical of a mild attack, and where not many of the leaflets actually drop off it has apparently little or no effect on the yield of latex.

Naturally all degrees in severity of attack may be observed, but the symptoms above described develop especially when infection occurs on very young leaves, 1 to 3 days old. According to Stahel (*23*), leaves more than a week old rarely become infected at all. Even before this the tissues have already become firm and more resistant to penetration by the fungus, so that the resulting lesions are quickly delimited, often somewhat hypertrophied, and usually small (1 to 4 millimeters in diameter), with sometimes a dead papery center. (Pls. IV and VI.) Although large numbers of these minute spots may develop on a single leaflet and cause considerable stunting, death rarely results.

The under surface of both large and small spots has at first, under moist weather conditions, a velvety grayish white appearance from the millions of spores (conidia) of the fungus produced on slender conidiophores arising from the diseased leaf tissues. Later, over the

center of the smaller spots or around the margins of the larger ones on the upper leaf surface, minute black points appear, which represent the further fruiting stages of the fungus. (Pls. V and VI.) On account of their position around the spots these little stromatic bodies often form nearly complete rings, which are very characteristic of this disease on full-grown leaves. (Pl. VI.)

Young twigs, flowers, fruits, leaf petioles, and fruit stalks are also attacked, causing black hypertrophied areas or cankers.

LIFE HISTORY AND DESCRIPTION OF THE CAUSAL FUNGUS

The South American leaf disease is caused by the fungus originally described as *Dothidella ulei* P. Hennings (*11*, p. 134; *12*, p. 254; *20*, p. 849; *25*, p. 318), of the family Dothideaceæ. The disagreement concerning its taxonomic position has already been mentioned under the review of literature. Since the limits of both families, Dothideaceæ and Sphaeriaceæ, to which it has been referred, are ill-defined and not based sufficiently on the developmental morphology of the fruiting bodies, the classification of more or less atypical forms, such as the present one, is naturally attended with uncertainties. Therefore, until more is known, the writer prefers to use the original name.

Dothidella ulei has three fruiting stages, earlier thought to represent different fungi, the identity of which, however, Stahel (*23*) was able to demonstrate beyond reasonable doubt by tracing their mycelial connection in the leaf. The first or conidial stage, belonging probably to the type genus Scolecotrichum, but referred also by some authors to the closely similar genera, Fusicladium (*13*) and Passalora (*1*), develops mainly on very young leaves or other tender succulent parts as petioles, flowers, flower stalks, and young twigs. On account of the great susceptibility of the tissues of these organs at this time and the enormous number of conidia which are produced, this stage of the fungus is probably entirely responsible for the rapid spread and destructive defoliation of the trees.

The conidia are readily carried by the wind from tree to tree. According to Stahel (*23*), who has worked out the method of penetration and infection, a conidium falling upon a very young leaf, for example, germinates and forms an expanded appressorium, from which an infection tube penetrates the cuticle and gains entrance to the tissues. Leaves more than a week old are no longer susceptible.

Germination and the successful penetration of the susceptible leaf can occur only after moisture has been present continuously for 10 to 12 hours, such as happens, for example, on a very dewy night. Once inside the leaf the fungus spreads in all directions, and after a period of about five days the first external symptoms of the disease may be observed. One to two days later conidiophores of the "primary Scolecotrichum stage" appear scattered individually over the surface, and new conidia are formed. Thus, in less than a week the fungus is able to reproduce itself, a fact which explains the very rapid spread of the disease under favorable conditions. Later, when those young diseased leaves not killed by the fungus have grown further and have acquired their green color, this primary stage in which the conidiophores are able to break through

individually is transformed into the "secondary Scolecotrichum stage," where only long many-celled conidiophores push up in compact clusters from a sort of subcuticular pseudoparenchyma.

When the infected leaf is barely full grown the second or pycnidial stage of the fungus appears. This belongs to the type genus Aposphaeria. The pycnidia occur only on the upper side as minute black points scattered individually over the leaf or arranged in characteristic fashion around the borders of tiny hypertrophied areas and dead spots. (Pl. VI.) The pycnidia may develop either from the pseudoparenchyma of the secondary conidial stage or arise independently. They are formed regularly on diseased internodes and fruits, but according to Stahel the pycnospores have been found incapable of infecting even the youngest leaf. Hence this stage of the fungus evidently plays no part in spreading the disease.

On approximately 2-months-old or fully grown moderately infected leaves there appears scattered among the pycnidia the third or perithecial stage (Dothidella), which arises in the same way and is indistinguishable from the pycnidial fructification without microscopic examination. On old leaves the perithecia predominate, but Stahel (*23*) does not consider them significant in spreading the disease. Fresh ascospores were unable to withstand drying in a desiccator for more than four to six hours. Although they germinated weakly in water in about two hours, they required 16 hours of continuous moisture to form appressoria and effect partial penetration of very young leaves sown with the spores and kept in a moist chamber. Sufficient penetration and invasion of the tissues to be termed infection were never obtained, but there were also apparently no tests made in which fresh ascospores were sown on leaves remaining attached to the plant. The disease has therefore never been reproduced experimentally from inoculations with ascospores, and Stahel has had to depend upon microscopic investigation to prove the relationship of the three spore forms. In summarizing these studies he states that the connection between the Scolecotrichum, the Aposphaeria, and the Melanopsammopsis (Dothidella) forms has been established beyond all doubt along anatomical lines. Since earlier workers had also observed the constant association of the last two fruiting forms and Stahel was able to find occasional traces of the first one on the original material described by Hennings, there is little ground for questioning his conclusion, in spite of the fact that it is based entirely on morphological evidence.

PERPETUATION AND SPREAD OF THE DISEASE

From the above account the importance of the conidial stage and dependence upon it for perpetuation of the disease, once it has obtained a foothold in a planting, is realized. Although this stage develops as a rule only on very young leaves and other immature organs, it sometimes continues to appear on older leaves where normally only pycnidial and perithecial stages are found. Such prolonged production of viable conidia doubtless enables the fungus to bridge over short periods when susceptible tissues are absent. In the Guianas this is usually unnecessary, because on account of the wide variation between different trees and even between different branches on the same tree in the time of their annual leaf change,

young leaves are present throughout the year. A continuous reserve of viable conidia is thus maintained.

Under the above conditions, a resistant resting stage to carry the fungus over unfavorable periods is hardly needed, but the importance of such a stage in dissemination over long distances and from one country to another is apparent. Since Stahel's infection studies with ascospores were few and gave only negative evidence, additional investigation employing different methods and ages of material is needed to determine the part played by the perithecial stage of the fungus in the perpetuation of the disease. Still more important is a knowledge of the longevity of the mycelium in twig lesions, of which nothing is known. In view of the present tendency to propagate the tree by bud grafting, the danger of possible spread of leaf disease by means of hibernating mycelium in lesions on the budwood is evident.

The fungus is probably never carried by the seed, because the pod lesions are superficial and adhering spores probably could not infect the hard mature seed coat. Since the fungus is apparently unable to maintain an independent saprophytic existence, the chances of its transmission over long distances other than in lesions of plant parts are very slight.

That the disease on the plantations in the Guianas originated from the wild Heveas is well illustrated in an instance cited by Stahel in 1919 (*24*), of which the following is a summary:

> From 1911 to 1915 a mining company at Lawa, on the upper Marowyne River, put out 40,000 trees of *Hevea brasiliensis*. Since the trees were grown from imported seeds and stumps and the estate was located some 200 kilometers distant from the nearest Para rubber planting, the chances of the disease being introduced were very slight. Although the estate was reported to be in a very healthy condition as late as 1917, collections of leaves received at Paramaribo showed the presence of the disease. According to the manager of the estate, nothing abnormal occurred until March, 1918, when as a result of heavy fog frequently covering several hilltops planted with rubber, the disease appeared in epidemic form and spread to the rest of the planting. In six months' time, as a result of repeated loss of the young leaves, one-third of all the trees died, and the remainder showed a hopeless condition. This very promising estate was therefore completely ruined in a half year's time and was subsequently deserted.

ENVIRONMENTAL INFLUENCES ON THE DISEASE

BIOLOGIC FACTORS

The establishment of pure stands of the rubber tree, which in its native habitat occurs scattered or in small groups amid the wild confusion of other jungle species, is apparently the major reason for the great damage from the leaf disease. Unfortunately, very little is known about the behavior of the disease in the jungle, although Kuyper (*13*) found it generally prevalent on the wild *Hevea guyanensis*. It seems reasonable to suppose that after long association in their native habitat the relations between parasite and host have reached a state of equilibrium which becomes unbalanced upon the establishment of the latter in pure stands. The greater proximity of the planted trees combined with their natural variability in leaf renewal favors directly the epidemic spread of the fungus. The possibility, suggested by Belgrave (*4*), that in its altered environment

the tree itself has changed or that the plantation trees are descended from unusually susceptible types also exists.

CLIMATIC FACTORS

The careful infection studies made by Stahel (*23*) with the fungus of the South American leaf disease indicate that its spread and severity are largely dependent upon certain climatic factors. The requisite conditions are not essentially different, however, from those which obtain through a large part of the year in all moist equatorial regions. They are, specifically, enough rain and wind to disseminate the spores and the presence of moisture on the plant continuously for a period of at least 10 to 12 hours, which are required for germination and infection. Abundant moisture is furnished in some localities by prolonged mists and fogs, but usually by heavy dews. It is only on clear quiet nights that the dew remains long enough to allow infection, and the disease has always been found to be more severe during the dry season. In British Guiana, on the contrary, Bodkin (Harrison *9*, p. 16) states that it is particularly virulent during protracted periods of heavy rainfall and assumes a milder form during relatively dry periods, the leaves remaining green though riddled with small holes. However, Stahel observed that during the average rainy period the actual surfaces of the plant were not continuously wet for a sufficient length of time to insure infection.

Any circumstance which hinders or delays dew formation reduces the amount of injury from the leaf disease. Wind is doubtless the most important single factor, but if it is too strong it has a deleterious effect on the growth of the tree (*10*, p. 6). The local alternating land-sea breezes which set up as a result of unequal heating of land and water operate ideally on unobstructed coastal areas in shortening the period of dew formation. The mature plantings of Hevea examined by the writer on the east coast of Trinidad probably in large part owe their relative freedom from the leaf disease to the prevalent night breezes, although the comparatively short wintering period is doubtless a contributing factor. The strong trades striking the Guiana coast, however, necessitated the leaving of protective belts of jungle, which have, as earlier indicated, favored the disease. On exposed sites in the same region the injury was always less.

Differences in soil apparently have little or no influence on the prevalence of the leaf disease.

POSSIBILITIES OF CONTROL

CONTROL IN INFECTED REGIONS

Numerous suggestions are offered in the literature for controlling the leaf disease. Although a good deal of money is said to have been expended by a few of the larger plantations in carrying out some of these suggestions, very little carefully controlled experimental work appears to have been done. The only measure which seems to have been finally adopted was to cut down the trees and replace them with more profitable crops. It was not learned to what extent this has been done; but it is known that many estates have been merely aban-

doned, to await the return of prices which will make further tapping under such conditions profitable.

Where the disease occurs on small plants or in the nursery the trials made by Bancroft (*2*), Stahel (*22*, *23*), and others indicate that it can be held in check by frequent spraying with Bordeaux mixture. On the plantation, however, spraying as an annual program is for obvious reasons impracticable. In this respect the South American leaf disease offers analogy to chestnut blight, in that the value of the individual tree is usually not sufficient to compensate for a schedule of treatment necessary to keep it free from the disease.

The method of control recommended by Stahel (*23*, p. 107), based on his studies of the fungus but apparently not as yet experimentally demonstrated, aims at eradication of the disease. According to him, since the disease is perpetuated entirely by the conidial stage, which can only infect the very young growth, by keeping all the trees free of this for a short period the conidia would not fall upon susceptible parts and would die. He therefore prescribes the cutting out of all the new shoots which appear during a period of three or four weeks over the entire plantation. To prevent reinfection adjacent estates would of course need to cooperate.

From preliminary trials Stahel estimates that no more labor would be required by this method than for spraying. He admits, however, that complete eradication is impossible, because of the wild Heveas and the long distances over which the wind could carry the conidia from them to the plantations. It is furthermore questionable whether the measure would be successful even when applied locally in view of our inadequate knowledge of the fungus.

The failure to find thus far a practicable method of control for the leaf disease is naturally discouraging, but emphasizes the need for further study of the problem. One important direction which such a study might take is toward the development of disease-resistant types. For this purpose attention is called to the promising possibilities which exist in the abandoned Guiana plantings. In a few severely diseased plantings inspected during this survey occasional trees were observed to be unaffected. Furthermore, after several years' observation of the disease in British Guiana, Bodkin (Harrison *9*, p. 16) states that in every cultivation attacked by the disease a few trees stand out prominently, having made excellent growth and having large heads clothed with healthy dark-green foliage, and that such trees appear to be immune to the disease. It is conceivable that within such a variable species as *Hevea brasiliensis* substantial differences in susceptibility occur, just as were demonstrated by the writer (*18*) in the case of the brown bast disease. The recent assurances of successfully propagating the rubber tree vegetatively make possible the preservation and rapid multiplication of any resistant type. The selection of such, however, will not be so simple as one might at first suppose, because characteristics other than resistance must be taken into account. The ideal would be, of course, to find types which combine a superior quality of rubber and a high yield with resistance. Careful study will be necessary, since the supposed resistance in many cases will prove to be only apparent and due to escape through coming into

leaf at a different time or to other factors. Nevertheless, the chances seem promising enough to warrant the attempt, and this should not be delayed, because many of the deserted plantings are gradually being cut down and replaced by other crops.

Until resistant strains are isolated or until further study has demonstrated a practicable method for preventing or controlling the leaf disease, the establishment of new plantings in the Guianas is not likely to be attempted. Although favorable localities in these regions might be selected, the disease will nevertheless be a latent menace to the enterprise.

EXCLUSION FROM NONINFECTED REGIONS BY QUARANTINE

Although at present it is scarcely advisable to plant Hevea in infected regions, there are doubtless extensive areas in other parts of the western Tropics equally suited to its culture. It is important, however, that these uninfected countries prevent the possible introduction of the disease by establishing suitable restrictions on the importation of propagating material. The general efficacy of quarantine measures has been sufficiently demonstrated with respect to other diseases not to require elaboration here. Since further natural spread of the disease is limited by sea and mountain barriers (see fig. 1), it is unlikely to reach other regions except through ocean commerce. Importations from the infected countries should be allowed, therefore, only under Government supervision and limited to seed and large "stumps," which do not carry the disease.

SUMMARY

The discouraging outcome of the formerly very promising rubber-plantation industry of the Guianas has been recognized for some time to have been largely due to the ravages of an endemic leaf disease which spread from the scattered wild trees of the jungle to the closely spaced plantings. In consequence of recent agitation for a near-by source of crude rubber, attention is again focused on the American Tropics and has naturally raised the question as to what extent this leaf disease will be a factor in contemplated enterprises. Since the trouble has been studied considerably in the past by local botanists, this bulletin presents mainly a review of the present situation obtained during a visit to the infected regions, a summary of the main facts known about the disease, and suggestions for future procedure.

The disease occurs apparently throughout the indigenous range of the genus Hevea, which includes Peru, Brazil, and the Guianas. It is also established on the island of Trinidad, having probably been imported along with propagating material.

The South American leaf disease is doubtless the most serious trouble which affects its cultivated host (*Hevea brasiliensis*). Through its injury to the foliage it not only makes tapping unremunerative but under favorable conditions repeated defoliations result in extensive die-back of the branches and actual death of large numbers of trees.

The amount of damage to the industry from the leaf disease in Trinidad has been much less than in the Guianas, owing probably

to differences in climate. Although in general it has doubtless been a discouraging factor, in the eastern section at least there have been no important losses to producing estates.

The rubber plantations of British Guiana and Dutch Guiana (Surinam) have been either largely abandoned or the trees cut down and replaced by more profitable crops. The leaf disease has been considered largely responsible, although the relatively high cost of labor was doubtless a contributing factor.

The most striking symptom of the disease occurs when the very young leaves blacken, wither, and fall off. Leaves less severely injured continue to grow, the larger spots becoming papery and torn. This, combined with stunting, gives the mature foliage a thin ragged appearance. The lower surface of the spots is at first velvety with conidiospores, and later, on the upper surface, black pycnidia and perithecia are often characteristically arranged in minute ringlets. On young twigs, fruit stalks, and other young organs black hypertrophied lesions are produced.

The causal fungus (*Dothidella ulei* P. Henn.) is known to possess conidial, pycnidial, and perithecial fruiting stages, although the first is almost entirely responsible for the rapid spread and defoliation of the trees. Only the very young leaves up to 7 days old are susceptible, and within a week after infection a new crop of conidia may be formed. According to Stahel, none of the spore forms are very resistant to drying; but further viability studies are needed, especially to determine the longevity of the mycelium in twig lesions.

The fungus, which is apparently an obligate parasite, is probably never carried by the seed or by large cut-back seedlings, or "stumps," since neither of these is susceptible to infection.

The optimum conditions for the epidemic spread of the leaf disease are (1) the continuous presence of young foliage and (2) abundance of moisture on the plant for a period of 10 to 12 hours, furnished sometimes by prolonged mist or fog but generally by heavy dews. Since the duration of the latter is greater on quiet, clear nights, the disease is generally more severe during the dry season of the year.

Of the numerous suggestions made in the past for controlling the leaf disease, none appears to have been practicable. The situation is not considered hopeless, however, because a sufficiently detailed knowledge of the disease as a necessary basis for control measures is lacking.

Attention is called to the promising possibilities existing in the deserted Guiana plantings for the selection of disease-resistant strains of the rubber tree. Until such strains are obtained or until further investigation has demonstrated a practicable method of prevention or control of the leaf disease, renewed planting in the infected regions, at least in the Guianas, is unlikely. Plantations may be established in other parts of the American Tropics, however, in regions where the disease does not exist and other conditions may be equally suitable for the growth of the tree. In this case effective restrictions on the importation of propagating material to prevent the introduction of the disease should be adopted.

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